A geometric model describing a quasi-equilibrium of energy flow in populations of stream insects

(growth/metabolism/bioenergetics/temperature/Ephemeroptera)

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ABSTRACT   Studies of growth, population structure, and metabolism for the mayfly nymph *Ephemerella dorothea* suggest that in natural streams this species maintains a nearly uniform weight-specific metabolic rate from the time of hatching (0.002 mg) to maturity (4.0 mg) as average stream temperature increases from 0.5° to 15°. The observed homeostasis represents a central tendency between two opposing factors that affect metabolism (size and temperature) and is achieved because any increase in metabolic rate due to warming of streams from winter to late spring is almost completely compensated by the increase in nymphal size from hatching to emergence. Results indicate that natural selective processes have favored individuals whose growth rates are proportional to seasonal changes in temperature. The model suggests a possible mechanism for explaining synchronous larval growth, pulsed adult emergence, and progressive decreases in adult weight of individuals emerging after the main cohort.

An intensive ecosystem study on a third-order tributary of White Clay Creek, Chester County, Pennsylvania, has yielded estimates of population growth, respiration, and production for major species of aquatic insects. Studies of growth, metabolic, and feeding rates, coupled with estimates of population density and weight structure, suggest an apparent tendency for uniform energy flow through the insect community during the year.

This tendency towards an equilibrium of energy flow is maintained, in part, by seasonal changes in available food resources and community structure of consumer organisms. Allochthonous detritus dominates the fall-winter food base; in spring and summer, algal production, mainly diatoms, is the principal energy source. In most streams, these resources overlap in all seasons but the relative proportions fluctuate seasonally. Insects are the major primary consumers in streams and have become highly specialized with respect to physical habitat, food resource, and season of activity (1). In White Clay Creek, microhabitat specialization combined with a diverse insect fauna permits continuous use of available food resources. This contributes to stability of nutrient cycling and uniformity of insect production.

In White Clay Creek, the same resource is utilized by several insect species in most microhabitats. The activity period of each species, however, is highly synchronous within species but out of phase temporally with the closest competitor of each species. Potential close competitors are often species within the same genus or members of allied genera. Thus, temporal segregation of species populations and trophic and physical resource partitioning appear to be the major factors leading to uniform energy flow and production in stream insect communities.

Uniformity of energy flow at the community level may de-

pend partially upon a quasi-equilibrium of energy flow in component species. This paper describes how a mayfly, *Ephemerella dorothea* Needham, maintains a uniform weight-specific metabolism during population growth over a wide range of temperatures. *E. dorothea* is active during the winter and spring and is distributed from Nova Scotia to Michigan, southward to Missouri and South Carolina (2). Mayflies of the genus *Ephemerella* are important components of the insect community in White Clay Creek.

MATERIALS AND METHODS

Oxygen uptake by *E. dorothea* was measured with a differential respirometer (3). Large random collections of nymphs were made from all habitats at 2-week intervals in a third-order tributary of White Clay Creek. Animals were kept at ambient stream temperature, sorted into size groups, and placed in respiration vessels within 2 hr of collection. Vessels contained sterilized gravel (2.0–4.0-mm particle size) and 8 ml of filtered (0.45-μm-diameter pores) stream water. Oxygen use was measured at 30-min intervals for 3 hr following a 2-hr period of equilibration. Depending upon body size and temperature, the number of animals per vessel varied from 2 to 30 in order to ensure that measurable amounts of oxygen were consumed. All nymphs in a given vessel were similar in size. Test animals were killed in hot water, dried for 48 hr at 60°, and weighed individually to the nearest μg.

Respiration rates of *E. dorothea* were measured at 5, 10, 13, 14, 15, 16, and 17°. Experiments were performed from November to May at temperatures nymphs were currently experiencing in the natural stream. In no case was respiration measured at temperatures outside the range of diel fluctuations expected on collection day. To estimate partitioning of assimilated energy by natural populations, this approach seems better than prolonged laboratory acclimation of animals at unrealistic temperatures.

Nymphs collected but not used for a respiration study were also dried and weighed. These weights were combined with those of experimental animals to compute the mean and range of weights for the population on a given date. Additional collections of *E. dorothea* were made at 2-week intervals to further describe population growth in White Clay Creek.

RESULTS AND DISCUSSION

Respiration rate for *E. dorothea* was highly dependent on body size and temperature (Table 1). A power function ($Q_{O_2} = aW^b$) provided the best fit for data relating respiration rate (Q_{O_2}) with nymphal dry weight (W). It appears that *E. dorothea* adheres to classic patterns for invertebrate metabolism (Fig. 1). These results show that: (*i*) oxygen consumption increased proportionally with temperature at a given body weight; (*ii*) small

Table 1.   Regression equations ($Y = aX^b$) and error statistics for estimating oxygen consumption at various stream temperatures

Stream temperature, °C	Population weight range, mg	a	b	s_b	r_{YX}
5	0.011–0.309	0.688	0.661	0.061	0.96
10	0.133–0.491	1.023	0.692	0.034	0.96
13	0.105–1.976	1.263	0.663	0.018	0.99
14	0.122–1.549	1.332	0.672	0.026	0.99
15	0.463–3.368	1.459	0.713	0.063	0.93
16	0.462–1.790	1.775	0.672	0.063	0.91
17	0.707–1.683	1.615	0.732	0.043	0.85

s_b is the standard error of b; r_{YX} is the correlation coefficient of Y on X.

nymphs have a higher metabolic rate per unit weight than larger nymphs; (*iii*) the Q_{10} approximates 2.0 throughout the normal activity range; and (*iv*) animals appear stressed at temperatures close to the upper lethal limit. Each line segment in this figure delimits the range of weights for the population at a given natural temperature regime (e.g., range of 0.1–0.5 mg when stream is 10°). Nymphal growth and adult emergence are highly synchronous in White Clay Creek (Fig. 2). Peak adult emergence occurs when stream water averages 15° (mid-May), and few nymphs are found when average stream temperatures exceed 17°.

Because temperatures range from 0 to 15° during nymphal growth, one expects *a priori* a large variance in metabolic activity. Data on weight-specific metabolism, however, show that the *E. dorothea* population is restricted to a narrow range (0.8–2.8 μl O_2 mg^{-1} hr^{-1}) at all immature growth stages (Fig. 3). Metabolic measurements were made only at temperatures which the animals were experiencing in the stream on the day of collection. This results in a positive correlation between the size of experimental animals and test temperature. Line segment length and solid dots in Fig. 3 depict the size range and average body weight, respectively, of the population at specific White Clay Creek temperatures. These data suggest a tendency for metabolic rates to remain unchanged for the main population cohort despite rising water temperatures during the spring. The analysis includes daily thermal changes because stream temperatures fluctuate diurnally (4–6) and invertebrate metabolism responds rapidly to these changes (7–12). For example, when the White Clay Creek averages 10°, the diel range

is about 7.5 to 12.5°. In this thermal regime, metabolism of the main cohort probably ranges from 1.2 to 2.1 μl O_2 mg^{-1} hr^{-1}, while the smallest and largest nymphs in the population broaden the range for the population as a whole (Fig. 4; 0.7–3.2 μl O_2 mg^{-1} hr^{-1}).

Results for *E. dorothea* suggest that seasonal fluctuations in metabolic rates are no greater than daily changes experienced throughout the nymphal growth period. This apparent homeostasis is maintained from the time of hatching (dry weight 2 μg; average temperature 2–4°) until adult emergence in mid-May (dry weight 2–4 mg; average temperature 15°). It would appear that growth rates of this species are adapted to seasonal temperature patterns so that weight-specific metabolism remains within narrow limits. Selection has apparently occurred for individuals whose growth tends to balance almost exactly the relationship between two opposing factors affecting metabolism: (*i*) increased metabolism with increased temperature, and (*ii*) the inverse relationship between body size and weight-specific metabolic rate.

Regression analysis was used to test whether a population maintains a balance or central tendency between the effects of temperature and body size on weight-specific metabolism. This analysis compared metabolic data gathered at all body sizes and temperatures throughout the growth period of the population. A regression coefficient not significantly positive suggests
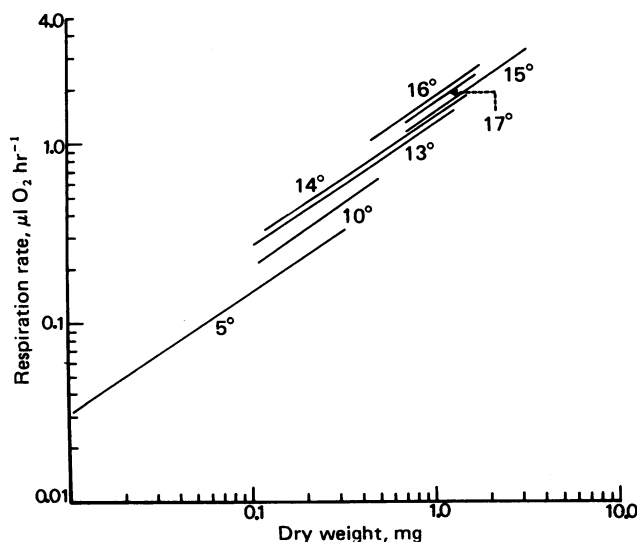

FIG. 1.   Respiration rates of *Ephemerella dorothea* nymphs at seven constant temperatures.
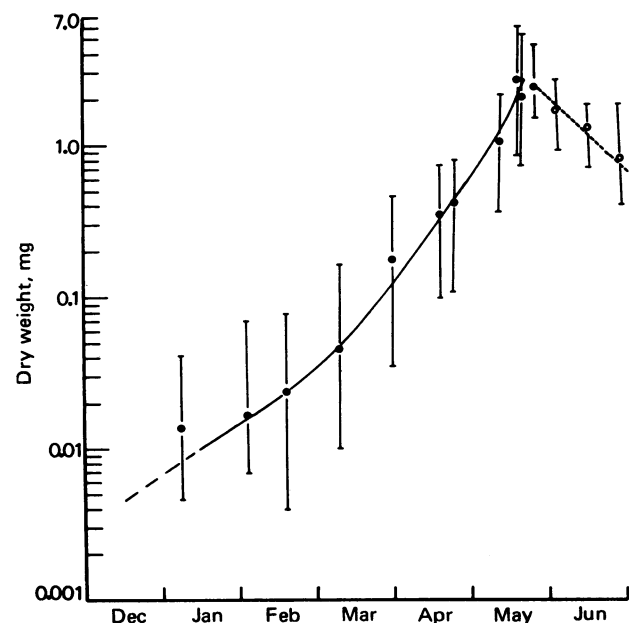

FIG. 2.   Average population growth of *Ephemerella dorothea*. Vertical bars delimit the weight range. Broken line connecting open circles is the average weight of subimagoes.

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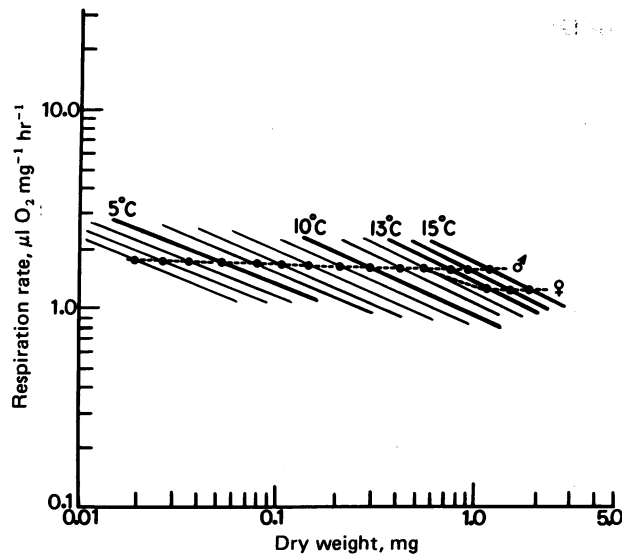*Proc. Natl. Acad. Sci. USA 75 (1978)*   383

FIG. 3. Weight-specific respiration of *Ephemerella dorothea* during nymphal development. The broken line connecting open circles indicates mean weight of nymphs at each stream temperature regime.

a tendency for metabolism to remain uniform during growth. Regression analysis was made for *Perlesta placida* Hagen, a predator stonefly in White Clay Creek. The almost horizontal regression (Fig. 5) suggests that weight-specific metabolism for this species remains almost uniform despite large changes in body size (Fig. 6) and temperature. The slightly negative slope indicates a partial overcompensation for increased stream temperatures. This may be due to a disproportionate increase in tissues with low metabolic activity (e. g., integument, mature oocytes) during nymphal growth. In Fig. 6, all nymphs weighing more than 4 mg are terminal instar females, which have large amounts of tissue with low activity. The above analysis is valid only when data for metabolism are measured: (*i*) at test temperatures close to ambient stream conditions at the time animals are collected, (*ii*) on animals not subjected to

FIG. 5. Linear regression analysis of weight-specific metabolism for *Perlesta placida*. Data obtained at different stages of growth and various temperatures (10, 13, 14, 15, 16, 17, and 20°) are combined in a single regression. The regression coefficient ($b = -0.238$) was not significantly different from zero ($t_{68} = 1.47$, $P > 0.10$).

prolonged exposure at seasonally unrealistic temperatures, and (*iii*) using the entire size range of animals present in a population on a given day.

The principal mechanism involved in keeping metabolism nearly uniform for the *E. dorothea* and *P. placida* populations is demonstrated in Fig. 7. Here weight-specific metabolism (μl O_2 mg^{-1} hr^{-1}) is plotted as a function of nymphal dry weight for three temperatures and superimposed are various theoretical pathways for growth of individual nymphs. Line segments A1 and A2 indicate the amount of growth required to keep weight-specific metabolism of the average cohort in a quasi-equilibrium during increases in stream temperature. When growth is kept proportional to seasonal changes in temperature, the energy demand per unit tissue remains constant throughout development. Failure to achieve sufficient growth due to inadequate food, increased competition, or density-independent factors results in increased metabolism as shown by line segments B1 and B2. With re-establishment of favorable conditions, growth rates may recover (B3) and again be proportional to increases in temperature. The new equilibrium, however, is accompanied by higher metabolic rates, a sacrifice in net
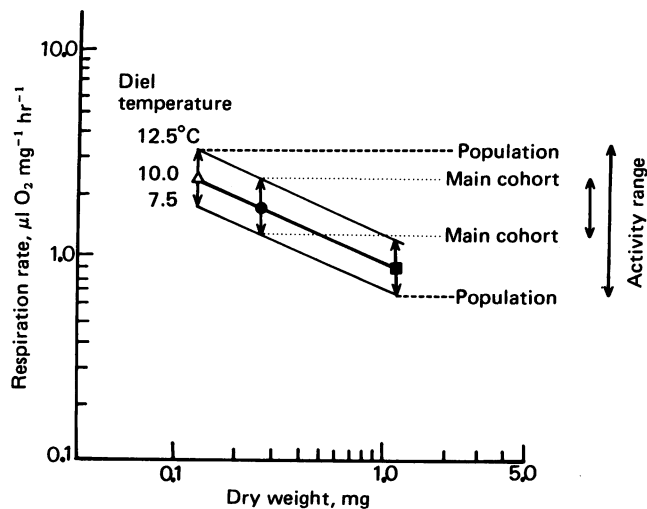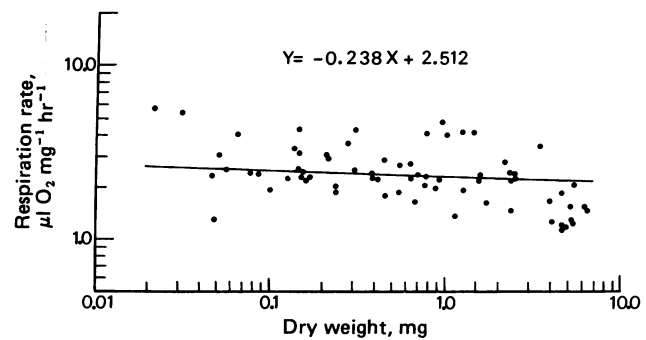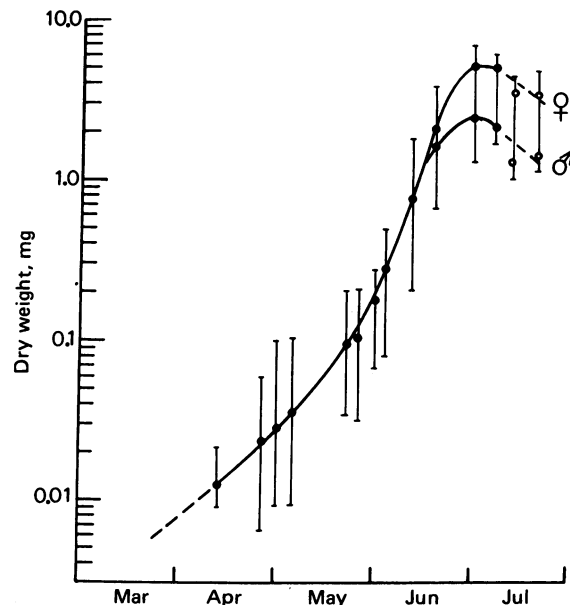

FIG. 4. Metabolic response of *Ephemerella dorothea* in a stream averaging 10° but pulsing from 7.5 to 12.5° diurnally. Heavy line depicts weight-specific metabolism at 10°; weight-specific metabolism at 7.5 and 12.5° was extrapolated from experiments at higher and lower temperatures. Arrows indicate diel range of metabolism for the smallest (△), main cohort (●), and largest (■) nymph in the population when stream temperatures average 10°.

FIG. 6. Population growth of *Perlesta placida* in White Clay Creek. ●, Nymphs; ○, adults. Vertical bars show the range of body sizes from qualitative samples.
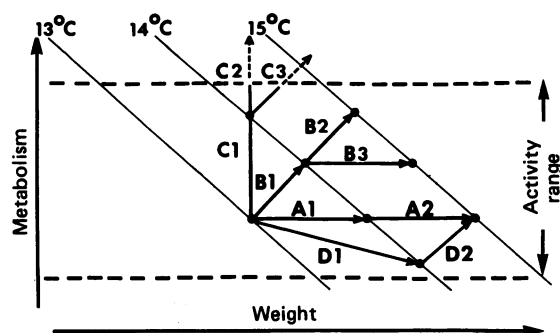
FIG. 7. Diagram outlining the weight-specific metabolism of *Ephemerella dorothea* as stream temperatures warm from 13 to 15°. Vectors **A–D** indicate various theorètical growth patterns.

growth efficiency (growth/assimilation), and produces smaller-sized adults with diminished fecundity (unpublished data). The main cohort, however, has a high net growth efficiency (65%) when weight-specific metabolism remains uniform (1.5 μl O_2 mg^{-1} hr^{-1}). Net growth efficiency deteriorates in parallel with growth lag and falls below 50% at the upper boundary of the activity range for metabolism. The rate of metabolism is elevated to high levels if no growth occurs during successive temperature increments (Fig. 7; C1–C3). Survival is probably low when metabolic rates exceed the normal activity range. This is supported by observations that: (*i*) nymphs in the natural population rarely exceed the respiration limits defined by the activity zone (Fig. 3); (*ii*) subimagoes emerging after the major cohort show an exponential decline in weight (Fig. 2; broken line) as predicted by the model; and (*iii*) the last nymphs to emerge as adults in early June produce few, if any, eggs.

In contrast, individuals whose growth exceeds the population average have a lower rate of weight-specific metabolism at comparable temperatures (D1). Reduced metabolism tends to slow growth and redirects the metabolic activity back to the middle of the range (D2).

The above "geometric" model suggests a possible explanation for the synchronous nymphal growth and adult emergence of many winter–spring insect species in White Clay Creek. In addition, the model implies that a decrease in the quality and/or quantity of food would lower growth rates below levels

needed to prevent abnormally high metabolic rates. Elevated metabolism reduces the energy available for individual growth, fecundity, and the secondary production of the stream ecosystem. In the absence of compensation, such as increased feeding rates or shifts in assimilation efficiency, growth lag under elevated metabolism may become more pronounced. This negative feedback might progressively elevate maintenance costs as the growth deficit enlarges.

The removal of riparian vegetation or additions of warm water effluents may accelerate the natural warming rate of streams. If growth rate optima or metabolic limits have evolved to conform to long-term temperature patterns, an increase in the rate of change and/or magnitude of seasonal temperatures may produce growth lag, elevate metabolic rates, and result in high mortality. Nymphs can maintain homeostasis in streams receiving thermal effluent only if growth rates accelerate and adjust to the new thermal regime. Accelerated growth, however, may advance emergence and expose adults to unfavorable air temperatures.

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